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Learning to appreciate others: Neural development of cognitive perspective taking

Dosch, M ; Loenneker, T ; Bucher, K ; Martin, E ; Klaver, P

Abstract: Neuroimaging studies have thoroughly investigated brain regions that are recruited when we put ourselves in another person's shoes. Taking a third-person perspective (3PP) as opposed to a first-person perspective (1PP) has been associated with brain activation in the inferior parietal cortex, the medial posterior cortex and the prefrontal cortex. Here we investigate for the first time the development of the neural network that yields cognitive perspective taking. Twelve adults (aged 25-32 years) and twelve school-aged children (aged 8-10 years) were investigated using functional magnetic resonance imaging (fMRI). Behaviorally, we found a decrease of reaction time differences between 3PP and 1PP with age indicating that adults were more efficient in processing a 3PP. Despite the reaction time differences both groups were equally accurate in their judgments. Brain imaging data indicated neural activity in the left inferior parietal cortex and precuneus for adults during 3PP as compared with 1PP judgments. Children additionally showed enhanced activity in the dorsolateral prefrontal cortex and the right inferior parietal cortex. We found a significant interaction between groups and brain activation in the right dorsolateral prefrontal cortex and in the right inferior parietal cortex. These results suggest that the development of the ability to reason about another person's mind accompanies a shift in activity from frontal to posterior brain regions and from bilateral to unilateral left inferior parietal cortex.

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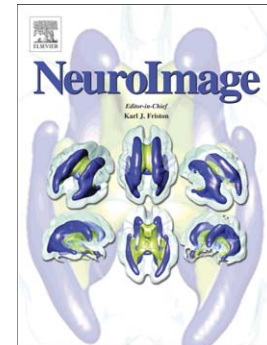
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Learning to appreciate others: Neural development of cognitive perspective taking**M. Dosch^a, T. Loenneker^{a,b}, K. Bucher^a, E. Martin^{a,b}, P. Klaver^a**

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INTRODUCTION

Since the beginning of this century neuroscience methods have been applied to the investigation of social cognition in adult subjects. Reasoning about other people's mind and understanding what they think, feel or believe requires the ability to step into their "mental shoes" and reason according to their perspective (Gallese et al., 1998). This is crucial for successful social interaction. Perspective taking includes the awareness of one's own subjective spatial and mental space (first-person perspective, 1PP) and the ability to ascribe visuo-spatial perspectives and mental states (cognitive or emotional states) to another person (third-person perspectives, 3PP). In the present study we investigate the ability to take another person's mental perspective.

Neuroimaging studies revealed brain regions that are active when we step into another person's mental perspective to represent his or her experience as compared to one's own. For instance, we take a 3PP when we try to appreciate what another person thinks about a particular topic or feels in a given situation. Taking the mental perspective of another person, as opposed to the own perspective has been associated with brain activation in the inferior parietal cortex, including the temporo-parietal junction (TPJ), medial posterior cortex (posterior cingulate/precuneus) and medial prefrontal cortex (David et al., 2006; Ruby et al., 2001, 2003, 2004; Vogeley et al., 2001). Furthermore neuropsychological evidence has also highlighted the importance of the inferior parietal cortex (IPC) and TPJ for perspective taking as well as for the distinction between self and other (Decety et al., 2003a). Direct cortical stimulation of the right IPC has induced the phenomenon of out of body experience in an epileptic patient (Blanke et al., 2002), and damage to this area can lead a patient to believe that his own body is controlled by external forces (Mesulam, 1981).

Despite the remarkable results from neuroscientific research on perspective taking in adults, little has been done so far to explore the neuronal development underlying these functions in

normal achieving children. Structural brain developmental studies have revealed changes in grey and white matter during late childhood, adolescence and even early adulthood. Both cross-sectional and longitudinal studies demonstrated that changes in frontal and parietal regions are especially pronounced and prolonged. Whereas white matter volume seems to increase linearly during the first two decades of life, grey matter development, particularly in posterior parietal and prefrontal cortices, increases from early childhood until about the age 12 (around the onset of puberty) and is followed by a decline during adolescence (Giedd et al., 1999; Gogtay et al., 2004; Sowell et al., 2003; Toga et al., 2006). While the nature and time course of structural changes during development have been described in detail, few studies focused on functional development. A general idea coming from studies on development of language and executive functions is that children show similar but more distributed pattern compared to adults. These findings have been referred to as focalization of neural development (Casey et al., 2005; Durston et al., 2006).

It is currently unknown how brain maturation influences the development of social cognition. Most research on the behavioral development of social cognition has been conducted in children between the age of 4-7 years (Astington, 1983, Baron-Cohen, 1993, Leslie, 1985), which indicates that major steps in social cognition are completed by that age. Although no study has investigated the neural development of perspective taking abilities, a handful fMRI studies investigate other social cognitive processes such as understanding irony (Wang, 2006), thinking about own intentions (Blakemore, 2006) or social-knowledge retrieval (Pfeifer, 2007). Among these studies, there seems to be some consistency with respect to the direction of change in prefrontal activity. In various frontal regions a decrease of activity with development was found particularly in the medial prefrontal and the inferior frontal cortex (for review see (Blakemore, 2008)).

Hence, on the basis of these structural and functional imaging results we hypothesize that the neural development of cognitive perspective taking is associated with changes in brain activity within the described neural network of social cognition involving posterior parietal regions (mainly the inferior parietal cortex) as well as prefrontal brain areas.

To test this hypothesis we developed a task requiring the appraisal of leisure activities from a third- or first-person perspective. Leisure activities are much more self-defining during childhood and adolescence than school activities because they provide more opportunity for self-direction and initiative than school performance activities. Self-defining activities tell children and adolescents something about “who they really are” or “what they are like” as a person and are therefore essential for the distinction between oneself and other persons (Larson, 2001). During the task short statements of real life situations were presented to both adults and children, who were required to make judgments for themselves and for another person who was introduced by a story. To assure that especially children adopt the mental perspective of another person and to keep the level of familiarity equal across all participants we chose a very different and unknown personality as a third-person. Choosing a third-person with very different characteristics allowed us to provoke qualitative differences between 1PP and 3PP judgments. To introduce participants with the other person we used a story of a child/adult with autistic behavior- we called him Paul. The story comprised his social behavior at home and during kindergarten and school time, his academic skills as well as his special interests. Participants did not know that Paul has been diagnosed as having Asperger’s syndrome nor did they know any other psychiatric diagnosis.

Since brain imaging as well as lesion studies on perspective taking in adults pointed to the importance of a fronto-parietal network, and structural studies showed that this network is not fully developed until early adulthood we expected that processing another person’s perspective would become increasingly efficient during development (decrease of reaction

times) and is associated with changes in brain activation within the prefrontal (particularly in the medial and inferior frontal) and the inferior parietal cortex. We further tested whether the development of perspective taking is supported by a focalization of the neural network involved in perspective taking by means of measures of variance and signal change of neural activity.

METHODS

Participants

Data were acquired from 12 children between 8.5 and 10.6 years of age (mean 10.0 years, 6 male) and 12 adults (aged 24.6-32.3, mean 29.1, 4 male). All children were recruited from public schools in the city of Zurich. Participants completed the German version of the autism-spectrum quotient questionnaire for adults or for children (AQ, Baron-Cohen, 2006) – a quantitative self-report instrument for assessing how many autistic traits a person has. None of the participants scored above the critical minimum of 30 out of 50 autistic traits (mean children: 18.73, mean adults: 16.35). No significant group differences ($t(1,21)=-1.19, p=0.249$) or sex differences were found ($t(1,21)=0.187, p=0.854$). Participants were also asked to indicate on an analogous scale (ranging from 0-100) how much they felt like Paul irrespective of sex. Female and males did not differ in their ratings (mean female=193, mean male=254, $t(1,22)=0.904, p=0.376$). Adult participants were university students. Four additional children had to be excluded due to extensive movement during the fMRI scanning (>5mm) and were therefore also excluded from behavioral analysis. All participants were right-handed as assessed by the Edinburgh Inventory Scale (Oldfield, 1971). None of the participants had a significant history of medical, psychiatric or neurological disorders on the basis of self- or parent-report. None of the participants used any neurotropic or psychotropic medication. Written informed consent was obtained from all participants, as well as written informed

parental consent for child participants. The study was approved by the local ethics committee and conducted in accordance with the guidelines set out in the Helsinki Declaration.

Task Description

Children were introduced to a virtual “other child” by reading a story about Paul a child with autistic behavior; adults likewise learned about a grown-up person with autistic behavior. During the fMRI measurement, the task required participants to make judgments about 32 leisure activities for themselves or for the other person. Activities with and without social interaction (with SI, no SI) were chosen to provoke differences in judgment for the 1PP and 3PP condition (assuming that Paul would dislike all social interactions). Separate task versions were created for children and for adults. The task employed a design in which the type of stimulus and the perspective taken by the participants were manipulated. In the self-perspective condition, subjects were asked to evaluate how much they like to do certain activities. In the other-perspective condition, subjects were instructed to imagine Paul and answer according to his preferences and interests and to ignore their own. In all trials, subjects were presented first with a picture of themselves or of Paul (duration 2 seconds) to indicate the perspective they had to adopt for answering the upcoming question. Subsequently, a sentence (e.g. ‘going to a friend’s birthday party’ or ‘reading a book’) was presented in black on a grey background (duration 6 seconds) together with a slider for answering, followed by a fixation cross (500 ms). Sixteen null-events in which only a fixation cross was shown were included and presented randomly. Participants were required to make their judgment by pressing the left or right button with the middle or index finger of their right hand. The button press moved a red marker on a slide on a continuous scale from left “I don’t like to do this activity at all” to right “I like to do this activity very much” (the scale range was from -100 to +100 with no visible scale in between). The longer the left/right button is pressed, the more the slider moves to the left/right side of the scale. The starting point of the red marker on the

continuous scale was presented randomly. Each of the four conditions (1PP with SI, 1PP no SI, 3PP with SI, 3PP no SI) consisted of 16 trials which had to be judged according to both perspectives (total 64 trials). The sequence of the trials was generated randomly for each participant. Each activity had to be judged for themselves as well as for Paul.

Experimental Procedure

Before the scanning session we took a picture of the participant and introduced him/her to Paul by showing a picture of him. Then, participants were instructed to learn about the other Paul by reading a story about a male child/adult with autistic behavior describing his social behavior, academic skills as well as his interests. Participants did not know that Paul has the diagnose of Asperger Syndrome.

We used different versions for adults and children. The difference between histories was that Paul's biography continued until adulthood for adults, but stopped at childhood (ca. 10 years) for the children. Similarly, the photograph of Paul was adapted to the age of the participants. The story comprised 200 words for children and 293 for adults. Participants were then asked to retell the story and answer several questions to ensure that they understood correctly and could imagine the Paul's personality. After introducing participant to Paul we carefully instructed them in the whole fMRI procedure and explained the task. Participants then practiced 5 trials from the 1PP and 5 from the 3PP. We again emphasized that it was very important to really try to imagine Paul and that we were interested in seeing how their brain works while they are thinking of him. We used MR-compatible video goggles to present the stimuli and additional acoustic noise protection by headphone (MRI Audio/Video System, Resonance Technology, Inc., USA) throughout the examinations. The task was programmed by Cogent implemented under MATLAB (<http://www.vislab.ucl.ac.uk/CogentGraphics/>)

MRI Data acquisition and analysis

BOLD sensitive images were collected on a 3.0 T General Electric MR-scanner using a gradient-echo EPI-sequence with a repetition time of 2000 ms and a 64x64 matrix. Altogether, 32 slices were aligned to the anterior and posterior commissure (flip angle = 50°, FOV = 24cm, slice thickness per volume = 3.8mm, 360 repetitions). Secondly, a three dimensional T1-weighted anatomical scan (FOV = 230 mm x 198 mm x 158 mm, matrix = 224x192x132; TR = 8.6 ms; TE = 2.1 ms) of the whole brain was acquired. Images were analyzed using SPM5 (Statistical Parametric Mapping software, Wellcome Department of Cognitive Neurology, London, UK, <http://www.fil.ion.ucl.ac.uk/spm>). The fMRI data were realigned and unwrapped for movement correction and were then normalized to a SPM template with a resampled voxel size of 3 mm³ and smoothed with a Gaussian kernel (full width at half maximum: 9mm).

For each participant the expected hemodynamic responses for each trial were modeled by two response functions, which were a canonical hemodynamic response function (HRF) and its temporal derivative. The functions were convolved with the event train of stimulus onset to create covariates in a general linear model. Misses were modeled as a parameter of no interest. Parameter estimates for four conditions (1PP with SI, 1PP no SI, 3PP with SI, 3PP no SI) were obtained by maximum-likelihood estimation while using a temporal high-pass filter (cut-off 128 s) and modeling temporal autocorrelation as an AR(1) process. Since neural development of perspective taking (1PP, 3PP) was the focus of our interest, we collapsed trials with and without social interaction. We added the analysis of the brain activation associated with the type of task (with SI, no SI) in the supplementary material.

In a voxel based analysis comparison between each condition and rest, and direct comparison between conditions were thresholded at $p < 0.05$ (FWE corrected, $k > 10$) and $p < 0.005$ (uncorrected, $k > 5$ voxels) for regions for which we had a strong a priori hypothesis, namely, the prefrontal and parietal cortex (Forman, 1995, Pfeiffer, 2007). To specifically look at developmental effects of perspective taking we calculated a ROI analysis on the basis of the

activation patterns from the main effect of 3PP and 1PP judgments. Because we have two independent groups the ROIs were based on the activation patterns across all participants (3PP > 1PP and 1PP > 3PP with a threshold of $p=0.005$, uncorrected, $k>5$ voxel). The children's and adults' data were compared in 12 regions of interest (ROI). According to these main effects 10-mm spheres around the local maxima of each significant cluster for each contrast (3PP>1PP and 1PP>3PP) were created using marsbar (<http://marsbar.sourceforge.net/>). Mean percent signal changes were taken from the raw data of every study participant for all conditions and activated voxels. For the contrast 3PP>1PP the following coordinates were taken to generate ROIs: left inferior frontal cortex ($x=-42$ $y=45$ $z=0$), right dorsolateral prefrontal cortex (middle frontal gyrus) ($x=39$, $y=24$, $z=27$), left inferior parietal cortex ($x=-36$, $y=-57$, $z=39$), right precuneus ($x=6$, $y=-69$, $z=39$), and right inferior parietal cortex ($x=39$, $y=-48$, $z=45$). For the contrast 1PP>3PP the following coordinates were taken to create ROIs: left posterior cingulate cortex ($x=-3$, $y=-33$, $z=42$ and $x=-6$, $y=-54$, $z=21$), anterior cingulate cortex ($x=0$, $y=15$, $z=-6$), left medial prefrontal cortex ($x=-9$, $y=48$, $z=9$), left middle frontal cortex ($x=-24$ $y=39$ $z=39$), left superior parietal lobule ($x=-27$, $y=-87$, $z=42$), right parahippocampal gyrus ($x=36$, $y=54$, $z=0$) and left middle temporal gyrus ($x=-57$, $y=-66$, $z=21$). For statistical analysis we used a repeated measure ANOVA with the within-subject factor perspective (1PP, 3PP) and the between-subject factor group (children, adults) for each ROI. To look after the potential effect of similarity between participants and Paul on brain responses, we correlated the ratings obtained from the participants with each ROI.

To examine whether the differences between children and adults in brain activation are caused by maturation rather than by performance differences in reaction times between groups, we separated the groups in good and bad performers. Using the median of reaction time performance for 3PP-judgments in both groups we built four groups. Thereafter brain activity within each ROI was analyzed using a repeated measure ANOVA with perspective (1PP,

3PP) as within-subject factor and age (adults, children) and performance (good-performer, bad-performer) as between-subject factors.

Current techniques of data analysis (e.g. SPM random effect second-level analysis) allow the identification of common areas of brain activation within a population. Since higher inter-individual variability is a principle characteristic of a developing population, we compared intersubject-variability of brain activation between children and adults. To visualize the inter-subject variability in location of brain activation we build probability maps in each group. A probability map is a measure of the spatial consistency of brain activation and shows how many subjects activated a particular voxel (Xiong et al., 2000). This technique allows for the identification of activation that is missed by group averaging and indicates what portion of the study population contributes to the overall group. To calculate the probability map for each group, we used one-sample T-maps for the contrast 3PP>1PP from each participant (threshold $p<0.05$, uncorrected). Using MRICron (<http://www.sph.sc.edu/comd/rorden/mricron>) we built the color scale which represents the percentage of subjects who activated for each voxel (ranging from 15%-100%). To further analyze the variability of brain activity, we estimated the nearest local maxima for each ROI-coordinate in each subject and calculated the standard deviation along the x-, y-, and z-coordinates of each group. The nearest individual local maxima had to be within the left parietal cortex for the ROI in the left inferior parietal cortex, the left and right precuneus for the ROI in the precuneus and in the right parietal cortex for the ROI in the right inferior parietal cortex. Otherwise it was excluded from analysis.

Euclidean distance values d around the mean location (x_0, y_0, z_0) for each selected ROI were also calculated for each subject using the following equation

$$\sqrt{(x_i - x_0)^2 + (y_i - y_0)^2 + (z_i - z_0)^2}$$

where x , y , and z are coordinates in MNI space for each individual (i). The Mann-Whitney U -Test was used to test for group differences in each ROI ($p<0.05$), because it is insensitive to

the assumption of independence of each coordinate. It is also more robust against violations of a normal distribution of population.

RESULTS

Behavioral Data

Judgments

Figure 1 shows the participants' judgments for the four conditions. With the selection of activities with and without social interaction (with, no SI) we provoked differences in judgment for self and other conditions. The results (Figure 1) show that both adult and child participants understood the task and performed successfully in terms of their appreciation of Paul's preferences: in the conditions where they had to judge whether Paul would like to do activities with social interactions their answers lay in the negative range whereas the answers for activities without interactions lay on the positive range. Repeated measures ANOVA with perspective (1PP, 3PP) and type of task (with SI, no SI) as within-subject factors and group (adults, children) as a between subjects factor revealed significant main effects of perspective ($F(1,22)=42.24$, $p<0.0001$) and type of task ($F(1,22)=25.88$, $p<0.0001$). There was no interaction between group and any condition (all $F(1,22)<0.144$, $p>0.707$).

Figure 1 about here

Reaction times:

Response times for judgments were analyzed using a repeated measures ANOVA with perspective (1PP, 3PP) and type of task (with SI, no SI) as within-subject factors and group

(adults, children) as a between subjects factor. There was a main effect for perspective ($F(1,22) = 27.4, p < 0.0001$), which indicated that judgments were made more slowly when participants had to answer according to the 3PP than when they had to answer for themselves. We further found a significant interaction between perspective and group ($F(1,22) = 5.7, p < 0.026$). Since there was no significant interaction between factors type of task (with SI, no SI) and perspective (1PP, 3PP) nor between the factors type of task and the group (children, adults) we collapsed trials with and without social interaction. Post hoc analysis showed that the difference between reaction times for 1PP and 3PP judgments (was significantly greater in children than in adults ($p = 0.03$, mean adults: 109 msec, mean children: 292 msec) and decreased significantly with age ($r = -0.043, p < 0.05$).

Neuroimaging Results

Main effect perspective: contrast 3PP versus 1PP judgments in children

Children showed enhanced activation in the parietal and frontal lobes during judgments for another person as compared with judgments for themselves (Table 1).

Within the parietal lobe, they activated the right and left inferior parietal cortex (BA 40), the post-central gyrus (BA 3) and the right precuneus (BA 7) and, within the frontal lobe, the right dorsolateral prefrontal (middle frontal gyrus, BA 9) and the left inferior prefrontal cortex (BA 46) and sublobar the right insula (BA 47).

Main effect perspective: contrast 3PP versus 1PP judgments in adults

In adults, the right precuneus (BA 7) and the left inferior parietal cortex (BA 40) were more activated during 3PP judgments than during 1PP judgments. No other areas showed significant activation.

Main effect perspective: contrast 1PP versus 3PP judgments

In children, the main effect of 1PP versus 3PP judgments revealed activation in the left anterior cingulate cortex (BA 32). Adults additionally activated the posterior cingulate cortex (BA 23, 24), left middle frontal gyrus (BA 8), and the left inferior parietal gyrus (BA 40).

Interactions: perspective by age-groups

Voxel-based whole-brain analysis revealed no significant brain activation for the interaction between perspective and group. We therefore performed ROI analysis.

Comparisons between children and adults

For the ROI analysis we took the activation pattern from the main effect 3PP versus 1PP judgments for all participants together as described in the methods. As can be seen in Figure 2 and 3a, adults and children showed comparable brain activity in all ROIs formed from the difference between 3PP and 1PP judgments, except for the right middle frontal cortex and in the right inferior parietal cortex. Using repeated measures ANOVA with the factor perspective (1PP, 3PP) and the between-subject factor group (children, adults) the statistical analyses revealed a significant interaction between group and perspective in right dorsolateral prefrontal cortex (middle frontal gyrus) ($F(1,22)=4.27, p<0.05$) and the right inferior parietal cortex ($F(1,22)=4.14, p<0.05$), but not in the other ROIs (all $F(1,22)<0.274, p>0.05$). The comparison between children and adults for the ROIs from the contrast 1PP versus 3PP judgment yielded no significant main effect of group (all $F(1,22)<1.68, p>0.208$ group interaction with any of the ROIs (all $F(1,22)<3.515, p>0.074$). We further analyzed the effect of similarity between the participants and Paul by correlating the ratings of similarity with percent signal change within each ROI. None of the ROIs correlated with similarity (all $r<0.329$).

Comparison between good and bad performers

To examine whether the differences between children and adults in brain activation are predominantly caused by maturation effects or by performance differences between groups, we

separated the groups into good and a bad performers (see methods). Brain activity within each ROI was analyzed using a repeated measure ANOVA with perspective (1PP, 3PP) as within-subject factor and age (adults, children) and performance (good-performer, bad-performer) as between-subject factors. Statistical analysis revealed no significant two-way and three-way interaction with performance in any brain region (all two-way interactions: $F(1,20) < 1.41$, $p > 0.248$) and all three-way interactions: $F(1,20) < 3.14$, $p > 0.092$),

Figure 2 about here

Figure 3A shows the probability maps for the contrast 3PP versus 1PP. The probability-maps suggest that children deploy a more extended neural network than adults. Within the frontal cortex, the activation seems to become more focal with development and in the more posterior regions we can see a shift from bilateral to unilateral left parietal activation. For the ROIs within the frontal lobule, we could not calculate the variability in location of individual local maxima because we had to exclude 5 from 12 adults since they did not show activity within the frontal lobule for the contrast 3PP>1PP. For the ROIs in the parietal lobule, the variability in location of individual local maxima did not seem to differ between groups (Figure 3B). We had to exclude six participants from the analysis because their data did not yield activation within our predefined search range (see methods): three within the left inferior parietal cortex (2 children, 1 adult), one within the precuneus (1 adult) and two within the right inferior parietal cortex (2 adults). If at all, adults showed a larger variation than children in the right parietal cortex.

This observation was confirmed in the analysis of the mean Euclidean distance values. The distances varied in these ROIs from 9.1 to 20.5 mm (see Fig. 3C). The Mann-Whitney *U*-Test showed no significant difference in Euclidean distances between the two groups in the left inferior parietal cortex ($p>0.76$, 2-tailed) and the precuneus ($p>0.109$, 2-tailed). Within the right inferior parietal cortex we found a tendency for a group difference in the Euclidian distance ($p<0.066$), indicating that adults showed larger variability (22.5 mm) than children (14.4 mm).

Table 1 and 2 about here (coordinates)

Figure 3 about here

DISCUSSION

Brain activation during participants' reasoning about another person's mind was compared with brain activity when they reflected upon their own preferences Reasoning about others, and understanding what they think, what they feel or what they believe involves stepping into their 'mental shoes' and taking their perspective. The ability to understand other people's mind and realize that they can have different perspectives is commonly referred to as having a "theory of mind". It requires the ability to distinguish "self" from "other" and appreciate another's person intentions, beliefs or preferences.

We would argue that cognitive perspective taking becomes increasingly efficient (decrease of ΔRT between 3PP and 1PP) after the age at which classic theory of mind tasks are accomplishable. Additionally, development of cognitive perspective taking shows changes in brain activity within a neural network involving particularly posterior parietal regions but also prefrontal brain areas. We would further argue that increased efficiency in perspective taking during development is supported by a focalization of the neural network involved. In contrast to previous imaging studies on cognitive development we were able to show by using measures of inter-subject variability analysis that children activated a coherent but more extended neural network during judgments for others than adults.

Maturation accompanies increased efficacy in perspective taking

There is currently considerable debate about the way in which we switch viewpoints from oneself to another person in everyday social interaction. According to the simulation theory, we place ourselves in another person's position by asking what we might believe or desire in a similar situation and simulate them (Taylor et al., 1994). Alternatively, the "theory-theory" claims that that we use a common sense psychological theory to understand other people's mind, rather than internally simulating them (Gopnik and Meltzoff, 1997). However, when taking another person's perspective it is not always sufficient only to simulate what *I myself* would do in the other person's situation. I need to imagine what the other person would do in her or his situation. In addition to "putting ourselves in another person's shoes" we therefore need to distinguish our own preferences from another person's intentions or preferences. Our behavioral data indicate that all participants, irrespective of age, inhibited their own egocentric perspective and mentally stepped outside their viewpoint to adopt the other person's preferences. Thus, in respect of this debate the ability to appreciate Paul's preferences appropriately cannot only be explained by the simulation theory. To appraise

Paul's preferences appropriately participants need to develop a 'theory' about the mind of a person like Paul.

Despite the qualitatively equivalent performance between children and adults, we quantitatively found a significant interaction in reaction times between group and perspective, which indicated that differences between self and other judgments decrease with age. The reaction time differences could not have been due to any differences in stimuli since we presented the same stimuli in both conditions. Several studies in adults have reported longer reaction times for 3PP than for 1PP (D'argembeau et al., 2007; David et al., 2006; Vogeley et al., 2004), although in some studies the differences were not significant (Ruby, 2003, 2004). In this context Choudhury and colleagues recently compared 3PP and 1PP reaction time differences between children, adolescents and adults (Choudhury et al., 2006). They also found a significant decrease in reaction time differences with age but in contrast to our findings the difference between 3PP and 1PP spread almost equally in both directions ($3PP > 1PP$ and $1PP > 3PP$), whereas none of our children showed faster reaction time for 3PP than for 1PP. Taken together, our behavioral results indicate that perspective taking in children seems to be generally established, but that their way of processing is less proficient than in adults.

Neural development of perspective taking

The focus of the present study was the development of the neural bases for processing other person's mental perspectives. The present data for 1PP processing are in good accordance with studies on neural correlates related to the self-processing and with self- perspective studies (Damasio et al., 2000; Piefke et al., 2003; Vogeley et al., 2004). Since we did not find any developmental differences in brain activity related to 1PP processing, subsequently only brain activation that is associated with 3PP processing will be discussed.

For 3PP compared to 1PP processing, adults activated the precuneus and the left inferior parietal cortex. Children additionally activated the left inferior frontal cortex, the right dorsolateral prefrontal cortex and the right parietal cortex. The significant interaction between age and perspective in the right dorsolateral prefrontal and in the right inferior parietal cortex indicates that these cortical regions play an important role in the development of perspective taking.

An increasing number of imaging (Ruby & Decety, 2001, 2003, 2004; Saxe, 2006; Saxe et al., 2005) and lesion studies in adults (Samson et al., 2004) point to the importance of the posterior parietal regions in relation to perspective taking. It has been proposed that the inferior parietal cortex is critical for the ability to distinguish between self and other (Decety et al., 2003b). This region was specifically involved when participants imagined another person being the agent of an action, imagined how another person feels in a given situation, what another person thinks or how another person experiences pain but not when they imagined these situations for themselves (Jackson et al., 2006; Ruby & Decety, 2001, 2003, 2004). Several studies in adults reported that the inferior parietal cortex in the right hemisphere was mainly involved in perspective taking whereas others found it more in the left hemisphere (David et al., 2006; Vogeley et al., 2004). Even clinical neuropsychology reported mixed findings. Samson and colleagues (Samson, 2004) reported evidence from three brain-damaged patients that the left TPJ is necessary for reasoning about other person's mind, while Blanke and colleagues (Blanke, 2002) referred to the importance of the right hemisphere. In the latter study direct cortical stimulation of this region induced an out-of-body experience, which is a 3PP of oneself. So far the contribution of each parietal lobule is still unclear since lateralization effects have not been investigated systematically. However, two recent studies demonstrated a selective impairment of self-other distinctions when repetitive transcranial magnetic stimulation (TMS) was applied over the right inferior parietal lobule as participants performed a perceptual task involving discrimination between photographs of themselves and

of a familiar face (Uddin et al., 2006). Self-other judgments on whole arm reaching movements (Preston et al., 2008) were also impaired when TMS was applied over the right but not over the left inferior parietal cortex. The additional 3PP specific activation in the right IPL in children compared with adults might therefore indicate that children need more self-other discrimination during 3PP processing than adults.

In comparison to adults, children additionally activated prefrontal brain regions during the processing of another person's perspective. The significant interaction between age and activation in the right dorsolateral prefrontal cortex indicated that only children specifically activated the right dorsolateral prefrontal cortex during 3PP.

Even though there are only a few studies on the development of the neural network underlying social cognitive processes, several authors reported a decrease of frontal activation with age. Using a similar task, Pfeiffer et al. (Pfeiffer et al., 2007) found the medial prefrontal cortex (mPFC) more activated in children than in adults while they reported whether short phrases described themselves or a highly familiar other person (Harry Potter). Another neuroimaging study found that the mPFC was more active in adolescents than in adults while participants were thinking about their own intention compared to thinking about physical causality (Blakemore et al., 2007). Because both of these studies focused on self-related processing comparison with our results is limited. Wang and colleagues investigated the development of the ability to understand irony, which requires the ability to separate the literal meaning of a comment from its intended meaning. Again, children and adolescents activated the mPFC and the left inferior frontal gyrus more than adults (Wang et al., 2006, 2007).

Thus, the present findings seem to be in line with the previous developmental studies in terms of the decrease of prefrontal brain activation. However, in contrast to the reported findings we mainly observed a decrease in activation within dorsolateral prefrontal cortex (DLPFC) instead of medial prefrontal cortex. The DLPFC is known to play a critical role in executive

function, particularly in cognitive control (Aron et al., 2004; Blasi et al., 2006; Bunge et al., 2002; Fecteau et al., 2007; Knoch et al., 2007; Knoch et al., 2006; Menon et al., 2001). From developmental psychology we know that higher cognitive control and attention functions develop long into adolescence (Davidson et al. 2006). Interestingly several social psychological studies have demonstrated that even adults frequently use self-knowledge as the primary basis for developing a model of what others know and feel, which has been described as a default mode of reasoning about others' mind. This egocentric bias can be interpreted as failure to suppress one's own perspective (Gilovich et al., 2002; Nickerson, 1999; Royzman et al., 2003; Vorauer et al., 1999). Considering this background the 3PP specific activation of the DLPFC in children may indicate that processing a 3PP requires children more than adults to inhibit their own prepotent egocentric perspective while they reason about Paul's perspective.

A possible explanation for the differences in brain activation in children compared to adults is cortical maturation, in particular grey matter reorganization and white matter increase throughout adolescence and early adulthood. Since the prefrontal cortex and the inferior parietal cortex are among the last brain regions to mature (Gogtay et al., 2004) it is plausible that these region contains less well functioning connections, leading to more activation for tasks that recruit them. Alternatively one can argue that more attention is needed by children to perform the task (judge according to Paul). Since we did not find performance related differences in brain activation we can rule out this argument.

In addition to the frontal and parietal cortex we found the precuneus to be specifically involved in 3PP processing in children and even more pronouncedly in adults. Several perspective taking studies found that the precuneus was activated during perspective taking. Its posterior part, which we found to be involved in 3PP processing, has recently been found to be preferentially activated during recollection of imagined rather than viewed items

(Lundstrom et al., 2005). Since participants did not personally know Paul and due to the fact that the story about him did not contain any explicit hint about how to answer the questions, they really had to imagine Paul's preferences rather than retrieve information from memory. The precuneus is also known as part of the so called "default network": A network of brain structures (including medial frontal, parietal and temporal areas) displaying the highest metabolic rates when participants are at rest but are 'deactivated' during cognitively effortful tasks (Gusnard et al., 2001; Raichle et al., 2001). However, in the context of our results its worth mentioning that there is a remarkable overlap between brain areas typically involved in social cognitive tasks and the 'default system'. Thus, it has been argued that the resemblance of brain regions engaged in social cognition as well as during "resting states" suggest that human beings might have a predisposition for social cognition to which they return when not explicitly forced to an effortful task (Schilbach et al., 2008). At this point we refer to Cavanna (2006) for review about the precuneus and its functional and behavioral correlates (Cavanna et al., 2006) and at Schilbach (2008) for an excellent overview about the relation between the default and the social cognitive networks of the brain.

Intersubject variability in location of brain activity

Previous neuroimaging studies on development, reported similar patterns of neural activation among children and adults, whilst children convey more distributed patterns of neural activation and a decrease of BOLD signal as compared to adults. Such a change in patterns of neural activity has been referred to as a focalization of neural development (Casey et al., 2005; Durston et al., 2006). The usual explanation for greater variation in neural activity across brain regions is that cognitive strategies are less efficient in children, whereas enhanced activity in focal brain areas during maturation has been interpreted as being due to increased efficiency and neural pruning. A problem, however, with interpreting focalization in brain imaging is that differences in neural activity can be confounded by differences in variability between groups: a more heterogeneous or incoherent pattern of neural activity not

only leads to a more distributed network but also to a reduction of neural activity. Thus, to determine if focalization of neural activity during maturation occurs, one has to disentangle measures of variance and measures of signal change (Berl et al., 2006; Xiong et al., 2000).

The probability-maps (figure 3a) showed that children deploy a more extended neural network than adults. Probability maps provide support for a developmental shift from frontal to posterior and from bilateral to unilateral within parietal activation. Since 5 adults did not show any frontal brain activation for the contrast 3PP>1PP, the comparison of the inter-subject variability in location of frontal brain activity between children and adults could not be calculated (figure 3b-c). In parietal areas, we found no indication for lower activation in children, while the probability maps indicate that children activate a more extended network than adults. Additionally, children showed a similar (or even reduced) degree of variance in the distribution of local maxima in neural activity as compared with adults. These findings suggest that children activated a coherent but more extended neural network of activity. This pattern of neural development is compatible with the hypothesis that an immature network has extensive activation because the network is not fully pruned. The findings do not support hypotheses on diffuse and dispersive networks in children, as has been suggested for different tasks (Berl, 2006, Durston, 2006).

Three potential weaknesses of the study should be mentioned: first, the significance of the study may be hampered due to the small sample sizes of the two groups. Second, the ability of taking another person's perspective may depend on the similarity or dissimilarity, respectively, of that person to the own personality which might have an impact on brain activation. We obtained the degree of similarity only by asking participants how much they feel alike Paul generally and did not find any significant correlations. For further studies, it would be interesting to explore the degree of similarity in more detail (for example by using a questionnaire) and investigate how it influences the ability to reason according to a third-person's perspective in children and adults and furthermore to explore its effect on brain

activation. In this context Mitchell (Mitchell et al., 2006) could show that a region in the mPFC linked to self-referential thoughts was activated during judgments according the perspective of a similar other person but not according a dissimilar other person. The overlap between judgments of self and a similar other person suggest that participants can use knowledge about themselves to infer the mental states of similar others. Moreover, since children show more difficulties in cognitive control, it would be interesting to explore the degree of self-suppression during perspective taking in dependence of the similarity to the other person. Third, according to Kriegeskorte (Kriegeskorte et al., 2009) there is a certain danger to commit a type I error by using the same dataset for statistical analysis and generating ROIs. Since we only built ROIs 1) after verifying our hypotheses about the brain location associated with processing a third-person's perspective (prefrontal cortex and inferior parietal cortex) and 2) for each significant cluster (there was no selection of clusters) we argue for the present approach. There would have been the possibility to built ROIs according to the literature to test our hypothesis. Since we were especially interested in developmental effects and there is no developmental study investigating perspective taking in children or adolescents, we would have missed important information by generating ROIs according to the adult literature. We nevertheless additionally performed a ROI analysis according to the literature. An adult study for our hypothesis about the parietal cortex brain activation and a developmental study for the hypothesis about the prefrontal cortex activation were used. The results confirmed our findings about the decrease of prefrontal cortex activation with age. In contrast to our ROI analysis in the right inferior parietal cortex there was no significant interaction between perspective and age-groups in the ROI of the right inferior parietal cortex based on the literature (see supplementary materials).

We conclude that the neuronal network underlying perspective taking is generally established in eight year old children: 1) because children showed no more variance within the adult neural network, 2) because the more widespread activation patterns cannot be explained by

greater inter-subject variance in children, 3) because the variability between areas within the children's network did not differ, and 4) differences in neural activity can be attributed to maturation, not to performance differences between adults and children. Children use a coherent but larger neural network to solve the task. One might speculate that children have not yet developed a specific approach to infer the perspective of others and thereby activated additional regions. Since adults are more experienced in social interaction with a variety of different personalities and thus are more skilled in perspective taking, they may have developed specific "modules" and use an efficient strategy to think about Paul's preferences, which presumably has been learned and reinforced from past experiences.

Taken together this is the first study on cognitive perspective taking in children that reveals the development of neural networks beyond the age of eight years. From developmental psychology studies we know that higher order cognitive function such as cognitive control develops into adolescence and is relevant in relation to a number of developmental disorders. The development of perspective taking abilities beyond six years of age is much less investigated, although respectful and considerate behavior cannot emerge without a sophisticated understanding of other people's perspectives.

The developmental differences we observed in this study cannot be attributed to qualitative performance differences since the behavioral output is the same in both age groups, but it seems that the children's strategy is less efficient (longer reaction times). Furthermore, we have been able to specify that neural development of perspective taking accompanies a shift of brain activity from frontal to posterior brain regions and from bilateral to unilateral left brain activation in the parietal lobule. This supports and extends the focalization model of neural development. Since the additionally activated right inferior parietal cortex in children did not show more inter-subject variability than the other brain areas, we conclude that children use a qualitatively different, but coherent network.

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Table 1
Peaks of Activity in Children and Adults during Direct Comparison of 1PP- and 3PP Processing.

Contrast	Area	coordinates					
		BA	x	y	z	t-	k
3PP > 1PP	Precuneus	31	21	-57	30	3.95	20
children	Inferior parietal gyrus	40	36	-39	42	3.82	28
		40	-36	-57	39	3.60	19
	Post-central gyrus	3	57	-18	33	3.39	8
	Middle frontal gryrus	9	48	27	33	3.71	37
	Insula	13	33	21	0	3.33	5
adults	precuneus	7	3	-72	48	4.24	81
	Inferior parietal gyrus	7	-33	-63	42	3.25	6
1PP > 3PP							
children	Anterior cingulate gyrus	32	-3	45	0	4.49	20
	Brainstem		3	-39	-39	4.32	10
adults	Anterior cingulate gyrus	32	-6	45	15	5.03	221
		24	9	27	15	4.10	9
	Cingulate gyrus	24	9	3	24	3.96	6
		32	-15	3	42	3.35	5
	Posterior cingulate gyrus	23	-12	-51	18	3.78	14
	Middle frontal gyrus	8	18	-15	63	3.74	39
	Inferior parietal gyrus	40	-57	-30	24	3.59	8

Clusters in a priori regions of interest and survive a threshold of $p < 0.005$ for magnitude, $k > 5$ voxels; All other clusters survive a threshold of $p < 0.05$; $k > 10$ voxels FWE corrected. BA=putative Brodmann's area; x, y, z =MNI coordinates; k=number of voxels in a cluster

Figure 1

A) This figure shows participants' judgments (mean and standard error) according the first-person and third-person perspective (1PP, 3PP) for activities with and without social interaction (with/no SI) B) Reaction times in msec for 1PP and 3PP and reaction time differences between 3PP and 1PP judgments are shown.

Figure 2 A-C

A-B) These figures show the main effect of 3PP versus 1PP judgments for all participants together. Statistical maps are thresholded at $p < 0.005$ and overlaid on a canonical T1 anatomical image. The signal change (%) and standard error of 1PP (light grey) and 3PP (dark grey) in the ROIs of the left parietal gyrus ($x = -36, y = -57, z = 39$), precuneus ($6, -69, 39$), right parietal gyrus ($39, -48, 45$), the left inferior frontal cortex ($x = -42, y = 45, z = 0$) and right dorsolateral prefrontal cortex ($x = 39, y = 24, z = 27$). Adults and children are shown separately.

Significant interactions (*) between perspective and group thresholded at $p < 0.05$.

C) This figure shows the main effect of 3PP versus 1PP for children (yellow), adults (red) and the overlap between children and adults (orange).

Figure 3A-C

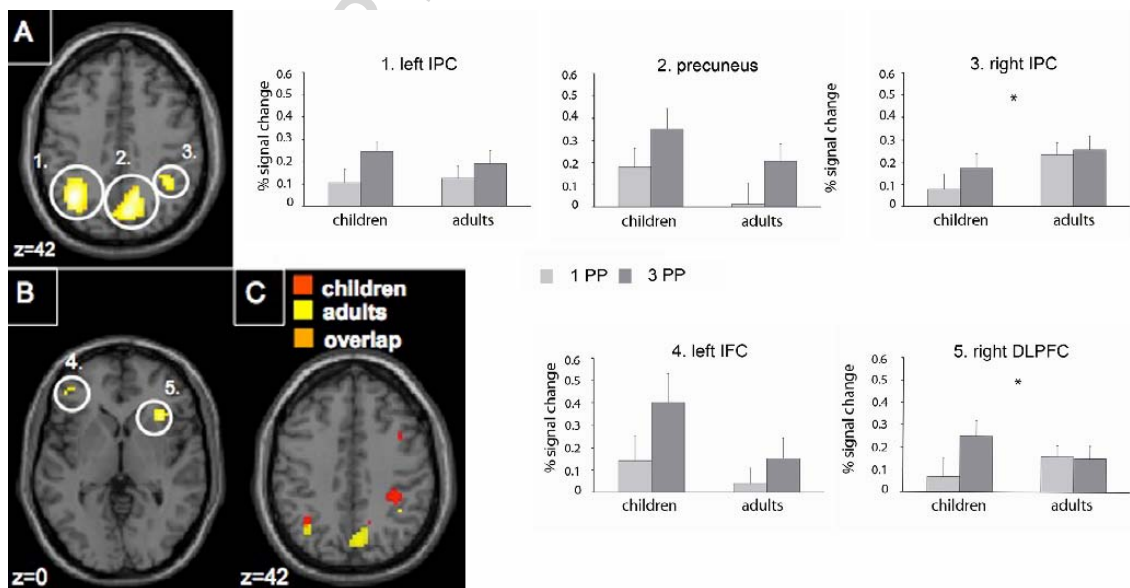
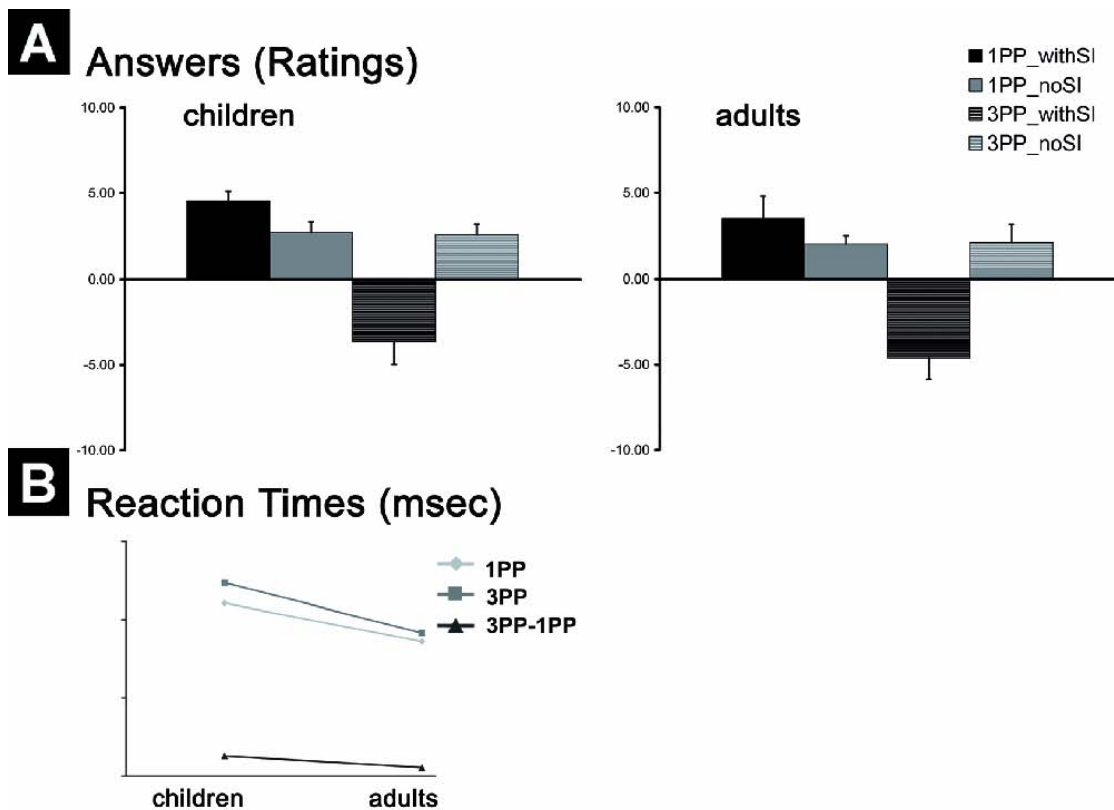
A) This figure shows the probability maps thresholded at $p < 0.05$ and overlaid on a canonical T1 anatomical image for children and adults separately for the contrast 3PP-1PP.

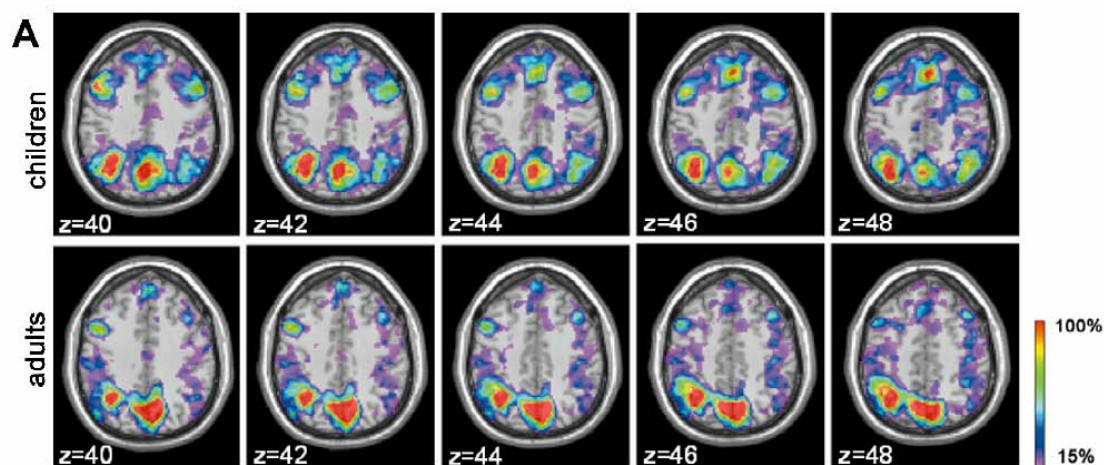
B) This figure shows the inter-subject variability in locations of activation (mm) for each region of interest 1) left inferior parietal cortex ($x = -36, y = -57, z = 39$); 2) precuneus ($6, -69, 39$); and right inferior parietal cortex ($39, -48, 45$). Each bar graph represents one standard deviation in x-, y-, and z-coordinates. C) Each bar graph represents the average Euclidean distance (mm) around the mean location for each brain region. The error bars represent standard errors.

Supplementary Material

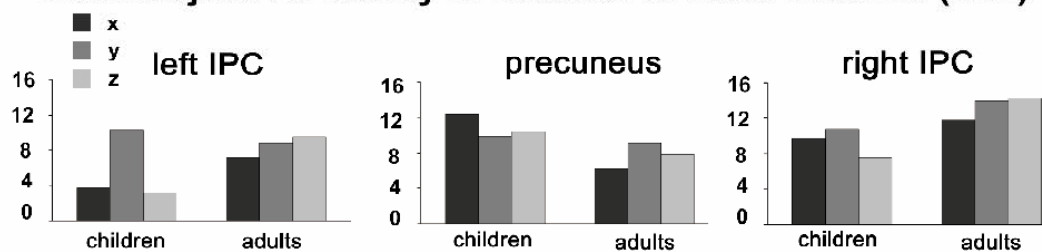
Figure 4-5

Figure 4 and 5 show the main effect of type of task (with SI, without SI) in children and adults. Statistical maps are thresholded at $t = 3.3, k > 10$ voxels and overlaid on a canonical T1 anatomical image





B Intersubject variability in location of local maxima (mm)



C Euclidean distance about the mean location (mm)

